Scientific Papers

Phylogenetic Relationships of Extant Pelobatoid Frogs (Anura: Pelobatoidea): Evidence from Adult Morphology

By

ANNE M. MAGLIA

Division of Herpetology, Natural History Museum and Biodiversity Research Center,
and Department of Ecology and Evolutionary Biology,
The University of Kansas, Lawrence, Kansas 66045-2454, USA

CONTENTS

ABSTRACT   The phylogenetic relationships of the Pelobatoidea, the most specious clade of basal anurans, are poorly understood. I conducted a phylogenetic analysis of 14 extant pelobatoid taxa (representing all recognized extant species of the family Pelobatidae and representative taxa of Megophryidae and Pelodytidae) and six outgroup taxa by examining alcohol-preserved specimens, dried skeletons, and cleared and double-stained skeletal preparations. Analysis of 73 characters from primarily adult morphology resulted in the discovery of six most parsimonious trees, each with 251

steps. The analysis supports Pelobatoidea and Pipoidea as sister taxa. Within the Pelobatoidea, Pelodytidae is the sister group to Pelobatidae, and Megophryidae is the sister taxon to [Pelobatidae + Pelodytidae]. Within the Pelobatidae, the monophyly of *Pelobates, Scaphiopus,* and *Spea* is supported. This paper summarizes and redefines morphological characters that historically have been used in the study of extant pelobatoid systematics and adds new, informative morphological characters. This should create a framework upon which further phylogenetic analyses of this group can be conducted.

RESUMEN   Las relaciones de parentesco de los Pelobatoidea, el grupo the anuros basales con más especies, son pobremente entendidas. Por medio del estudio de especímenes preservados, esqueletos secos y esqueletos transparentados y doblemente teñidos, conduje un análisis filogenético de 14 taxones vivientes de pelobatoideos (representando todas las especies vivientes conocidas de la familia Pelobatidae y taxones representativos de Megophryidae y Pelodytidae) y seis grupos externos. El análisis de 73 caracteres tomados fundamentalmente de la morfología adulta resultó en el descubrimiento de seis árboles más parsimónicos de 251 pasos cada uno. El análisis respalda a Pelobatoidea y Pipoidea como grupos hermanos. Dentro de Pelobatoidea, Pelodytidae es el grupo hermano de Pelobatidae mientras que Megophryidae es el grupo hermano de [Pelobatidae + Pelodytidae]. Dentro de Pelobatidae, la monofilia de *Pelobates, Scaphiopus* y *Spea* está bien sustentada. Este trabajo resume y redefine los caracteres morfológicos que históricamente han sido usados en el estudio de la sistemática de pelobatoideos actuales, y agrega nuevos caracteres morfológicos. Esto debería crear un marco sobre el cual otros análisis filogenéticos de este grupo puedan ser realizados.

INTRODUCTION

The Pelobatoidea, comprising about 95 extant species (Frost, 1985) in three families (Pelobatidae, Megophryidae, and Pelodytidae), is the largest and arguably, the most poorly studied group of basal anurans. These frogs are distributed throughout the Holarctic Region and extend into the Old World tropics (Duellman and Trueb, 1986). The pelobatoids also are represented by an extensive fossil record ranging from Late Jurassic of North America (Evans and Milner, 1993) to the Pleistocene of North America; the fossils include †*Eopelobates,* †*Macropelobates,* †*Miopelodytes,* and †*Tephrodytes.*

Although there are numerous suggestions as to the phylogenetic placement of the pelobatoids among other anurans (e.g., Brattstrom, 1957; Griffiths, 1963; Lynch, 1973; Cannatella, 1985), few studies have focused specifically on pelobatoid systematics. Henrici (1994) conducted the most inclusive phylogenetic analysis of the pelobatoids to date by examining both fossil and Recent forms. Her analysis resolved relationships among genera, but did not address the placement of the pelobatoids relative to other anurans or the relationships within genera. Cannatella (1985) included the extant pelobatoids in his analysis of archaeobatrachian frogs. Using adult anatomy and tadpole life-history characters, he was able to provide some reso-

lution to the phylogenetic placement of the pelobatoids among other anurans; however, many of his characters were not informative in resolving relationships within Pelobatoidea. Those characters pertinent to pelobatoid relationships provided little resolution beyond the family level, and when the results of his analysis were reported later (Ford and Cannatella, 1993), the relationships among the pelobatoid families were unresolved. Lathrop's (1997) subsequent reanalysis of a portion of Cannatella's (1985) data provided suggestions as to the among-genera relationships, but it did not address the placement of the pelobatoids among other anurans, and it was not able to elucidate some of the relationships within the family Pelobatidae. Therefore, there is a pressing need to understand the phylogenetic relationships of the extant pelobatoids, including their relationships with other frogs and their inter- and intrafamilial relationships.

Currently, a separate study in progress (Amy Lathrop, pers. comm.) is designed to address the generic relationships within the pelobatoid family Megophryidae. To reduce overlap in efforts, the focus of the present paper is threefold—(1) to understand the relationships of the Pelobatoidea with other anurans; (2) to determine the familial-level relationships within the group; and (3) to hy-

pothesize relationships of taxa within the family Pelobatidae. Herein, I use morphological characters to conduct a phylogenetic analysis of extant pelobatoids. A detailed description and comparison of the adult pelobatid skeleton have been presented elsewhere (Maglia, in press) and should serve as a companion to this analysis. Within the pelobatoids, I included two representative taxa of the family Megophryidae, one representative taxon of Pelodytidae, and representatives of all currently recognized extant taxa of Pelobatidae. Because the phylogenetic placement of pelobatoids is problematic, I included several taxa representing the Pipoidea, Discoglossidae, Bombinatoridae, and Neobatrachia (*sensu* Ford and Cannatella, 1993) that serve as outgroups.

HISTORICAL TAXONOMY OF THE PELOBATOIDS

Since Noble (1931) placed the pelobatoids into the suborder Anomocoela (which he considered to be an intermediate between pipids and bufonids), the systematic placement of the pelobatoids has been contentious. Brattstrom (1957) also allocated the pelobatoids to the suborder Anomocoela (Fig. 1) based on skeletal morphology and available fossil data. He argued that the pelobatoids are characterized by procoelous vertebrae, a condition he hypothesized to be derived by fusion of the intervertebral cartilages in primitive discoglossids. Reig (1958) erected four suborders—Aglossa (pipids); Amphicoela (leiopelmatids); Archaeobatrachia (pelobatoids, discoglossids, and rhinophrynids); and Neobatrachia (all other frogs). Griffiths (1963) suggested that the pelobatoids are intermediate between primitive and advanced frogs based on the characters of the epicoracoid horns, sternal apparatus, depressor mandibulae muscles, and squamosal bones. He also suggested that the pelobatoids and rhinophrynids are closely related and, together, represented an early side branch of the line of arciferal frogs that diverged from the pipids.

One of the earliest phylogenetic analyses of anuran relationships using parsimony was performed by Inger (1967), whose morphological analysis indicated that Pelobatoidea is the sister group to neobatrachians, except Microhylidae, which is the sister group to the clade [Neobatrachia + Pelobatoidea] (Fig. 1). In his analysis, the rhinophrynids are the sister group to the clade [neobatrachians + pelobatoids + microhylids], and the pipids are the sister group to this combined clade. Kluge and Farris (1969) (Fig. 1) also used parsimony analysis to suggest that the pelobatoids are the sister group to all neobatrachians (including microhylids). Their analysis suggested that [pipids + rhinophrynids] are the sister group to the clade [neobatrachians + pelobatoids].

Lynch (1973) hypothesized that the pelobatoids are a transitional group between archaic and advanced frogs and

do not form a monophyletic group. He argued that Pelobatidae (including what is now Megophryidae, *sensu* Cannatella, 1985) is the sister group to Neobatrachia, and Pelodytidae is the sister to this combined group (Fig. 1). He also suggested that Pipidae is the sister group to the clade [(Neobatrachia + Pelobatidae) + Pelodytidae]. Duellman (1975, 1988) and Duellman and Trueb (1986) asserted, based on the incomplete nature of the cricoid cartilage, that Pelobatidae (including Megophryidae) and Pelodytidae are sister groups (Fig. 1). They also showed that, together, these taxa form the sister group of Neobatrachia, based on the following synapomorphies: (1) absence of ribs (also absent in Rhinophrynidae); (2) nonoverlap of the scapula by the clavicle; and (3) absence of the neopalatine bone. Using molecular evidence, Hay et al. (1995) hypothesized that Pelobatidae (including Megophryinae) and Pelodytidae are sister-taxa and that together they form the sister group to a clade comprising all other archaeobatrachians.

Based on the state of the trigeminal and facial nerves, Sokol (1977) proposed a classification that divides Anura into two suborders, Discoglossoidei (including only the families Leiopelmatidae and Discoglossidae) and Ranoidei (all other frogs). He suggested that although pipoids were considered to be primitive (e.g., Orton, 1953; Starrett, 1973), they actually may be a highly derived, indirect branch of the pelobatoids. He suggested that they evolved from an intermediate group with a pipoid-like tadpole, called "eopipoids." Laurent (1979), in an attempt to recognize the distinctiveness of the pelobatoids without drastically altering the existing nomenclature of Archaeobatrachia and Neobatrachia, tried to combine the findings of Sokol (1977) with the classification of Duellman (1975) by erecting the suborder Mesobatrachia to include Pipoidea (pipids + rhinophrynids) and Pelobatoidea.

Roček (1980) compared the development of the cranium of *Pelobates fuscus* to several other species of pelobatoids. Taking into account a single character, the developmental pattern of the tectum synoticum, he erected a classification of anurans composed of Archaeosalientia (containing †*Eopelobates* and *Pelobates*) and Neosalientia (containing all other frogs). However, this hypothesis has been criticized (e.g., Cannatella, 1985) because it takes a less than parsimonious view of anuran evolution.

The most thorough analysis of archaeobatrachian relationships is that of Cannatella (1985) (Fig. 1). His results suggested that Pelobatoidea is monophyletic and that the pelobatoids and pipoids are sister groups, and he suggested that Mesobatrachia (Laurent, 1979; = Pipoidei of Dubois, 1983) is monophyletic. Five synapomorphies (all with some level of homoplasy) unite members of Mesobatrachia; these are as follows: (1) hyale in two parts;
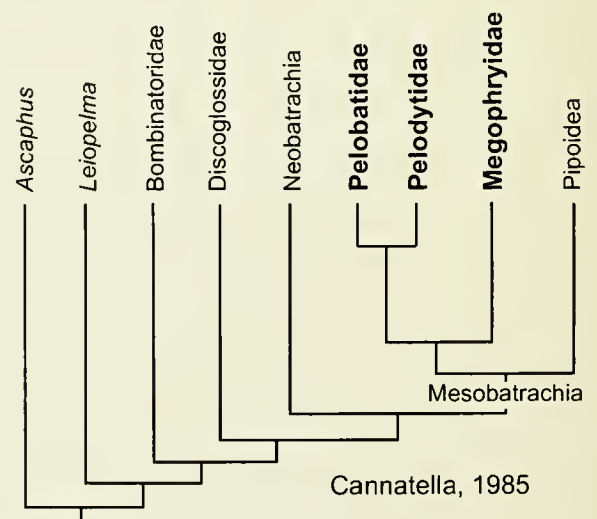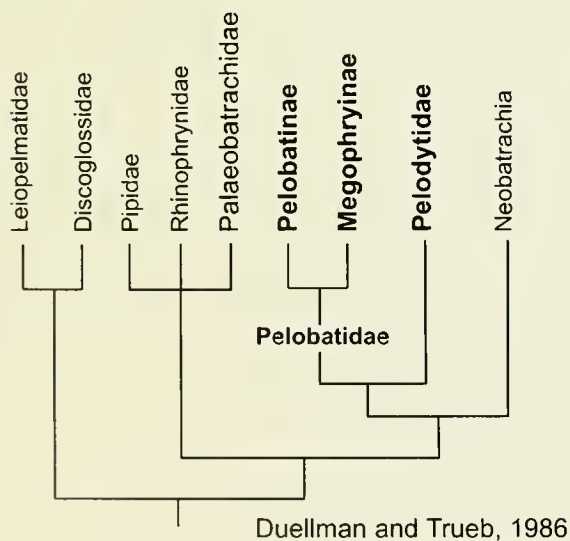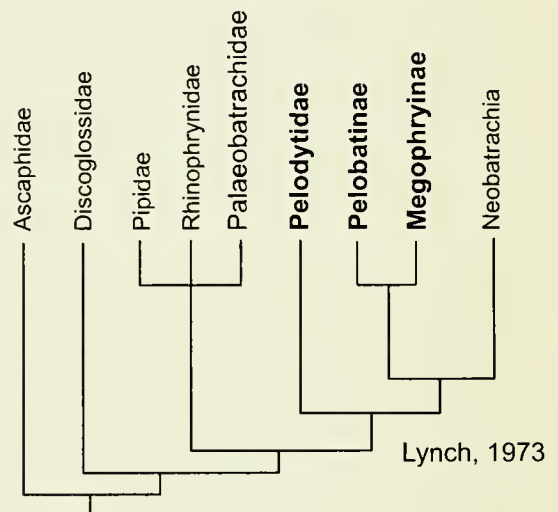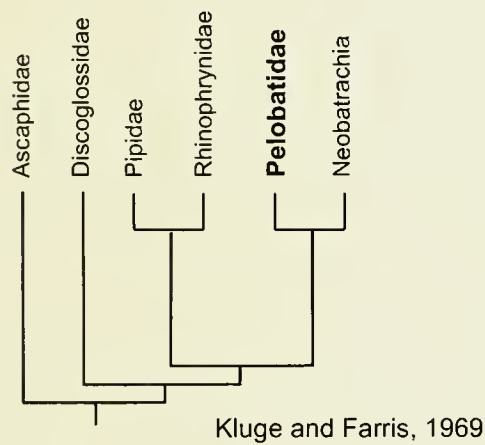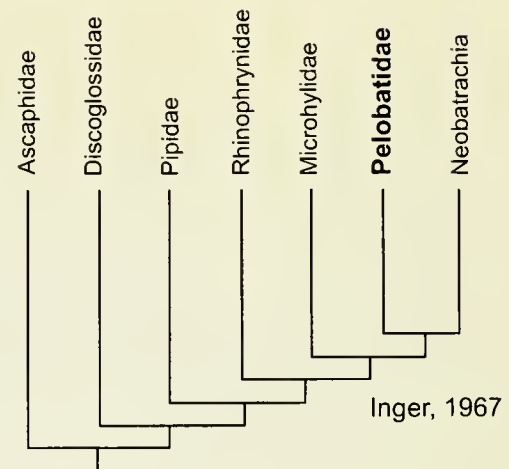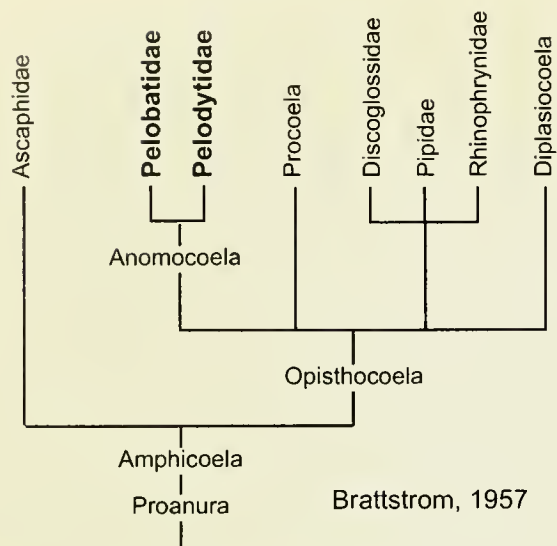
Fig. 1.   Some of the various hypotheses of anuran relationships that include pelobatoid taxa (boldface).

(2) cutaneous origin of the gracilis minor muscle; (3) hyoglossal sinus partially bound by laminae of hyalae; (4) presence of an accessory head of the gracilis minor muscle; and (5) concealment of the frontoparietal fontanelle. Cannatella's (1985) analysis did not provide resolution for familial-level relationships within the Pelobatoidea. Although the phylogeny resulting from his analysis depicts [(Pelobatidae + *Pelodytes*) + Megophryidae], he stressed that this was a result of his choice of equally parsimonious topologies and not the single most parsimonious result.

Reanalysis of Cannatella's data set by Hillis (1991) indicated that the pelobatoids are paraphyletic, and that the neobatrachians are the sister group to Megophryidae. He also hypothesized that the clade [Neobatrachia + Megophryidae] is the sister group to the clade [Pelodytidae + Pelobatidae], and this combined clade is the sister taxon to the pipoids. A second reanalysis of a portion of Cannatella's (1985) data set was conducted by Lathrop (1997). The hypothesis resulting from her analysis suggests that within Pelobatoidea, Megophryidae and Pelobatidae are sister taxa, and *Pelodytes* is the sister to this combined

clade. It also suggests that within Pelobatidae, *Spea* and *Scaphiopus* are sister taxa, and *Pelobates* is the sister to [*Scaphiopus* + *Spea*]. These results are consistent with those of Henrici's (1994) phylogenetic analysis of Recent and fossil pelobatoids. She proposed that Pelodytidae and Pelobatidae are sister groups, and recognized Pelobatinae and Megophryinae as sister taxa within the family Pelobatidae.

MATERIALS AND METHODS

CLADISTIC METHODOLOGY

Characters were coded for 20 taxa representing 11 species in the family Pelobatidae, two species in the family Megophryidae, one species in the family Pelodytidae, and six outgroup taxa (Pipidae: *Rhinophrynus dorsalis, Xenopus laevis;* Neobatrachia: *Leptodactylus fuscus, Limnodynastes fletcheri;* Discoglossidae: *Discoglossus sardus;* Bombinatoridae: *Bombina orientalis*). I examined alcohol-preserved specimens, dried skeletons, and cleared and double-stained skeletal preparations.

Seventy-three characters from adult and larval morphology were defined and included in the analysis. Although several characters are similar to those used by Cannatella (1985) and other authors (e.g., Henrici, 1994; Kluge, 1966; Zweifel, 1956), most characters were redefined and coded directly from specimens for this analysis. Ten characters were taken directly from the literature—Characters 64–72 (myology and soft tissue) were taken from Cannatella (1985), and Character 32 (condition of the stapes) was taken from Lathrop (1997). Character descriptions and illustrations are presented in the next section; the data matrix is presented in Appendix.

The monophyly of Pelobatoidea was assumed based on (1) ossification of the sternum, (2) presence of palatine process of the pars facialis of the maxilla, and (3) presence of adductor longus muscle (Cannatella, 1985). I forced the pelobatoids to be monophyletic, as well as forcing the monophyly of the pipoid outgroup (two taxa represented) and the neobatrachian outgroup (two taxa represented)

(Fig. 2). A phylogenetic analysis was performed using PAUP Ver. 3.1.1 (Swofford, 1993) using ACCTRAN optimizations; all transformation series were weighted equally and were treated as unordered. An heuristic search was performed with the topological constraint presented in Figure 2. The resulting tree was rooted using the discoglossid taxon, *Discoglossus sardus*, and the bombinatorid taxon, *Bombina orientalis*, the most basal outgroup taxa included in this analysis (according to the hypotheses of anuran relationships of Duellman and Trueb [1986] and Ford and Cannatella [1993]).
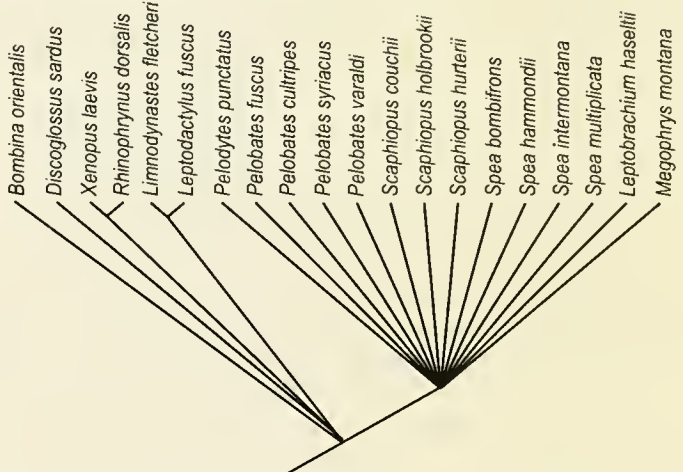

Fig. 2. Topology used to constrain analysis of data matrix. Note that the monophyly of the Pelobatoidea, Pipoidea, and Neobatrachia was not tested.

To determine robustness of support for each of the nodes, I calculated Bremer decay indices (Bremer, 1988; 1994) by rerunning the analysis several times, saving all trees one step longer than the previous analysis, computing the consensus, and then comparing the results to the results of the original analysis. I also calculated boostrap values for each of the resolved clades.

SPECIMENS EXAMINED

Institutions are as follows: American Museum of Natural History (AMNH), University of Kansas Natural History Museum (KU), Harvard University Museum of Comparative Zoology (MCZ), Museo Nacional de Ciencias Naturales, Madrid (MNCN), United States National Museum (USNM).

Spea multiplicata (KU 27622, 86662, 86664), *S. bombifrons* (KU 5405, 73382), *S. hammondii* (KU 176016), *S. intermontana* (KU 79436, 204563), *Scaphiopus couchii* (KU 20444, 73384, 209575), *S. holbrookii* (KU 20439, 145413), *S. hurterii* (KU 20472, 60173, 90096), *Pelobates cultripes* (KU 148619, MNCN 20041; MNCN 20241), *P. fuscus* (KU 68819, 129240), *P. syriacus* (KU 146856), *P. varaldii* (AMNH 62935, MCZ 31970), *Megophrys montana* (MCZ 22635, KU 79010), *Leptobrachium haseltii* (KU 194712), *Pelodytes punctatus* (KU 153435, 129241, MCZ 1616b), *Rhinophrynus dorsalis* (KU 69084, 168799), *Xenopus laevis* (KU 195934, MCZ 26585), *Limnodynastes fletcheri* (KU 186780), *Leptodactylus fuscus* (KU 92957, 166429, 167677, 167678), *Bombina orientalis* (KU 38645, 38649, 129703), and *Discoglossus sardus* (KU 183734, 129239, USNM 10052).

DESCRIPTION OF CHARACTERS

The 73 characters used in this analysis are described below. Refer to Maglia (in press), Wiens (1989), and Roček (1980) for additional descriptions and illustrations of pelobatoid osteology.

CRANIAL CHARACTERS (Fig. 3)

Frontoparietal

1. Ornamentation.—I considered this to be distinctive bony ornamentation of the frontoparietals, nasals, maxillae, premaxillae, and squamosals.

    0: dermal ornamentation absent
    1: dermal ornamentation present

2. Supraorbital flange.—This small, lateral expansion along the dorsolateral margin of the frontoparietal is a thin sheet of bone that forms a partial roof over the orbit and is best viewed in ventral aspect.

    0: supraorbital flange absent
    1: supraorbital flange present

3. Medial contact of frontoparietals.—The frontoparietals are either separate from one another, in contact for part or all of their medial margins, or are fused. Fusion is with or without a visible median suture. In *Pelobates*, the frontoparietals fuse with no median suture; however, Roček (1980) found that, developmentally, this arises from three separate centers of ossification (different from the state in *Xenopus* and *Rhynophrynus*).

    0: frontoparietals not in contact
    1: frontoparietals in contact posteriorly only
    2: frontoparietals in contact for most of medial margins
    3: frontoparietals fused, suture visible
    4: frontoparietals fused, no suture visible, two centers of ossification
    5: frontoparietals fused, no suture visible, three centers of ossification

4. Frontoparietal contact with nasal.—The anterior and/or anterolateral margin of the frontoparietal extends to abut or overlap the nasal.

    0: frontoparietal and nasal not in contact
    1: frontoparietal and nasal in contact

5. Occipital foramen.—In the taxa considered, the pathway for the occipital vessels is unroofed, and thus the vessels merely traverse the dorsal surface of the posterolateral corner of the frontoparietal, or it is roofed in bone to form a canal (= occipital foramen) through the posterolateral corner of the frontoparietal (Fig. 3).

    0: pathway for occipital vessels open
    1: pathway for occipital vessels roofed in bone

6. Frontoparietal boss.—In a few *Spea*, this raised ridge of bone is present in the anterior interorbital region. See Wiens (1989) and Zweifel (1956) for more thorough descriptions of this morphology.

    0: frontoparietal boss absent
    1: frontoparietal boss present

7. Lateral foramen.—In *Pelobates*, there is a large foramen in the dorsal third of the lamina perpendicularis, the portion of the frontoparietal that contributes to the lateral wall of the braincase.

    0: lateral foramen absent
    1: lateral foramen present

Nasal

8. Medial contact of nasals.

    0: nasals not in contact
    1: nasals in contact

9. Extent of posterior divergence of nasals.—In all taxa considered, the nasals diverge laterally from one another posteriorly. This divergence is minimal, involving only the posteriormost margins, or extensive, in-
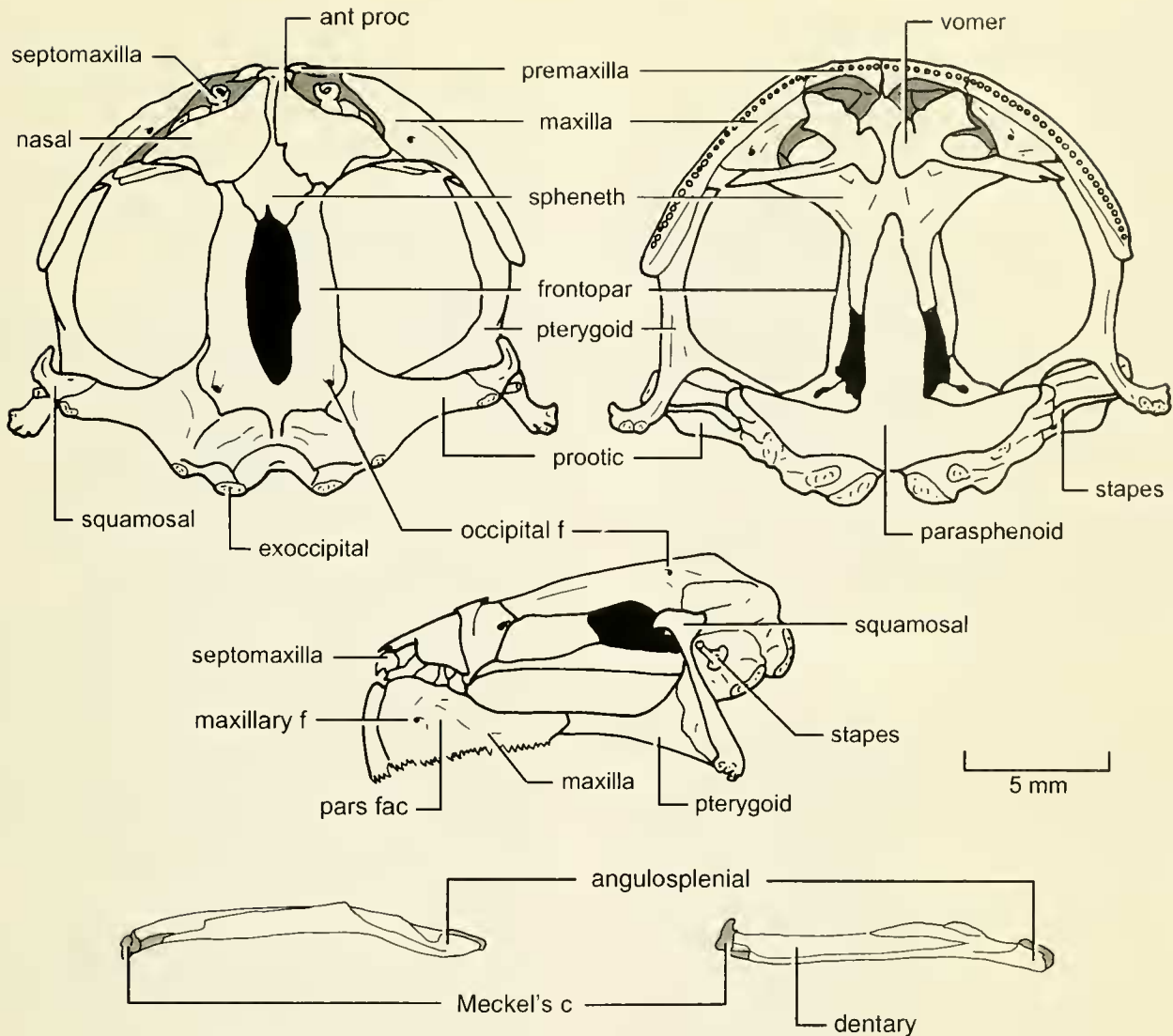
Fig. 3.   Cranium of *Spea multiplicata* (KU 86662) in dorsal (top left), ventral (top right) and lateral (center) views. Mandible is shown in lingual (bottom left) and labial (bottom right) views. Gray denotes cartilage, black denotes foramina. Abbreviations: ant proc = anterior process of nasal; c = cartilage; pars fac = pars facialis of maxilla; f = foramen; frontopar = frontoparietal; spheneth = sphenethmoid. Adapted from Maglia (in press).

volving at least half of the length of the nasal bones.

0: posterolateral divergence of nasals minimal (less than one third the length of nasals)

1: posterolateral divergence of nasals extensive (at least half the length of the nasals)

10. Shape of anterior process.—The anterior margin of the nasal forms a thin, blunt, rounded process that overlies the septum nasi, except in *Spea*, in which it forms a sharp point (e.g., Fig. 3).

0: anterior process of nasal blunt

1: anterior process of nasal pointed

11. Maxillary process of nasal.—In some taxa, the nasal possesses a lateral sheet of bone, the maxillary pro-

cess, that extends ventrally toward the pars facialis of the maxilla.

0: maxillary process of the nasal absent

1: maxillary process of the nasal present

Premaxilla

12. Width of alary process.—In anterior view, the alary process of the premaxilla is either thin (less than a fourth the width of the premaxilla) or wide (at least a third the width of the premaxilla).

0: alary process one fourth or less width of premaxilla

1: alary process one third or greater width of premaxilla

13. Premaxilla articulation with maxilla.—In ventral view, the premaxilla either abuts the maxilla or forms a small

posterior projection, the lingual process (Mendelson, et al., in press), that lies medial to the lingual margin of the maxilla.

    0: premaxilla abuts maxilla, no lingual process present
    1: premaxilla medially overlaps maxilla, lingual process present

14. Shape of pars palatina.—The pars palatina of the premaxilla is either of uniform depth (Fig. 3), or it broadens laterally.

    0: pars palatina of premaxilla nearly uniform depth
    1: pars palatina of premaxilla broadens laterally

15. Number of premaxillary teeth.—In the taxa considered, the average number of premaxillary teeth ranges from nine to 20.

    0:   9 premaxillary teeth
    1: 11 premaxillary teeth
    2: 12 premaxillary teeth
    3: 13 premaxillary teeth
    4: 15 premaxillary teeth
    5: 16 premaxillary teeth
    6: 18 premaxillary teeth
    7: 19 premaxillary teeth
    8: 20 premaxillary teeth

16. Height of alary process.—In anterior view, the alary process of the premaxilla extends dorsally to the level of the anterodorsal margin of the maxilla or beyond the margin of the maxilla.

    0: alary process extends dorsally to the level of the maxilla
    1: alary process extends dorsally beyond the level of maxilla

17. Condition of septum nasi.—The septum nasi is either cartilaginous or ossified for at least half of its length; in some taxa, the anterior margin forms a small plate that extends dorsoventrally between the alary cartilages of the nasal capsule.

    0: septum nasi cartilaginous
    1: septum nasi ossified for at least half its length
    2: septum nasi ossified, forming plate anteriorly

Maxilla

18. Posterior extent of maxilla.—In ventral view, the maxilla extends posteriorly to a level equal to about half the length of the orbit (Fig. 3) or extends posteriorly for more than three fourths the length of the orbit.

    0: maxilla not extending posteriorly beyond half the length of the orbit
    1: maxilla extending posteriorly for most of the length of the orbit

19. Number of maxillary teeth.—The average number of maxillary teeth ranges from 23 to 85.

    0: 23 maxillary teeth
    1: 25 maxillary teeth
    2: 26 maxillary teeth
    3: 33 maxillary teeth
    4: 35 maxillary teeth
    5: 40 maxillary teeth
    6: 42 maxillary teeth
    7: 48 maxillary teeth
    8: 50 maxillary teeth
    9: 85 maxillary teeth

20. Postorbital process.—This is a small process that extends dorsally from the maxilla just posterior to the orbit.

    0: postorbital process of the maxilla absent
    1: postorbital process of the maxilla present

21. Preorbital process.—This is a small process that extends dorsally from the maxilla just anterior to the orbit.

    0: preorbital process of the maxilla absent
    1: preorbital process of the maxilla present

22. Pars facialis.—This is a sheet of bone in the anterior portion of the maxilla that extends dorsally to invest the lateral margin of the planum antorbitale (Fig. 3).

    0: pars facialis of the maxilla absent (or poorly developed)
    1: pars facialis of the maxilla present

23. Maxillary foramen.—This small foramen pierces the pars facialis of the maxilla (or the underlying connective tissue if the pars facialis is absent).

    0: absent
    1: present

24. Pterygoid process.—In ventral view, this small process extends posteromedially from the pars palatina of the maxilla to articulate with the anterior ramus of the pterygoid.

    0: absent
    1: present

25. Palatine process.—This is a small process that extends medially from the pars facialis of the maxilla to ventrally invest the planum antorbitale. Although this has been considered to be the neopalatine (= palatine) fused to the maxilla by some authors (e.g., Zweifel, 1956; Roček, 1980), Wiens (1989:49) described the ontogeny of this element and showed that it is part of the maxilla.

    0: not distinct from vomer
    1: distinct from vomer
    2: absent

Parasphenoid

26. Ridge on body.—When present, this is a raised, V-shaped ridge on the posteromedial parasphenoid.

0: parasphenoid ridge absent
1: parasphenoid ridge present

27. Posteromedial process.—This small process extends posteriorly from the body of the parasphenoid; in some taxa, it overlaps the ventromedial margin of the foramen magnum.

0: posteromedial process of parasphenoid absent
1: posteromedial process of parasphenoid present

Vomer

28. Postchoanal process.—This process extends laterally from the body of the vomer to invest ventrally the planum antorbitale. When elongate, it comes into contact with the palatine process of the pars facialis of the maxilla in some taxa.

0: postchoanal process of vomer absent
1: postchoanal process of vomer short
2: postchoanal process of vomer elongate

29. Dentigerous process of vomer.—Among the taxa considered, the relative position of the tooth-bearing portion of the vomer varies.

0: dentigerous process of vomer anterior to posterior margin of planum antorbitale
1: dentigerous process of vomer at the level of posterior margin of planum antorbitale

30. Number of vomerine teeth.—The average number of vomerine teeth varies from zero to 15.

0: no zomerine teeth
1: 3 vomerine teeth
2: 4 vomerine teeth
3: 5 vomerine teeth
4: 6 vomerine teeth
5: 7 vomerine teeth
6: 8 vomerine teeth
7. 9 vomerine teeth
8: 14 vomerine teeth
9: 15 vomerine teeth

Prootic/exoccipital

31. Anterior margin of prootic foramen.—In the taxa considered, the posterior margin of the prootic foramen is always formed by bone. However, the anterior half may be formed completely by cartilage, formed by bone except for the most anterior portion, or formed completely by bone.

0: anterior margin of prootic foramen completely formed by cartilage
1: anterior margin of prootic foramen partially formed by bone
2: anterior margin of prootic foramen completely formed by bone

Plectral apparatus

32. Condition of stapes.—This character was taken from Lathrop's (1997) reanalysis of Cannatella's (1985) data.

0: stapes absent
1: stapes present, extending entire length of ear cavity
2: stapes greatly elongate (much longer than ear cavity)
3: stapes reduced (not extending length of ear cavity)

Pterygoid

33. Ventral flange of anterior ramus.—In some taxa, there is a thin, sheetlike process that extends ventrally for much of the posterior half of the anterior ramus of the pterygoid.

0: ventral flange of pterygoid absent
1: ventral flange of pterygoid present

34. Auxiliary dorsal process.—The pterygoid articulates with the maxilla by simply abutting it via the lateral margin of the anterior ramus, or it has a secondary articulation via a small auxiliary dorsal process that extends from the dorsolateral margin of the anterior ramus. See Mendelson et al. (in press:fig. A2) for illustration and further discussion of this character in other taxa.

0: absent
1: present

Squamosal

35. Condition of zygomatic ramus.—The zygomatic ramus of the squamosal, when present, extends anteroventrally from the region of the crista parotica. The ramus is short or long; when long, it articulates with the maxilla (in most taxa).

0: zygomatic ramus of the squamosal absent
1: zygomatic ramus of the squamosal short
2: zygomatic ramus of the squamosal long (half or more distance to dentigerous process of maxilla)

36. Condition of the otic ramus of the squamosal.—The otic ramus of the squamosal barely overlaps the crista parotica or forms an otic plate that invests most of the lateral half of the crista parotica.

0: otic ramus barely overlapping lateral margin of crista parotica
1: otic ramus forming otic plate

37. Squamosal contact with frontoparietal.—In some taxa, the frontoparietal and squamosal each possess platelike postorbital processes that may articulate dorsal to the otic capsule.

0: frontoparietal and squamosal not in contact
1: frontoparietal and squamosal in contact

Quadratojugal

38. Quadratojugal.—In some taxa, the quadratojugal is absent from the maxillary arcade.
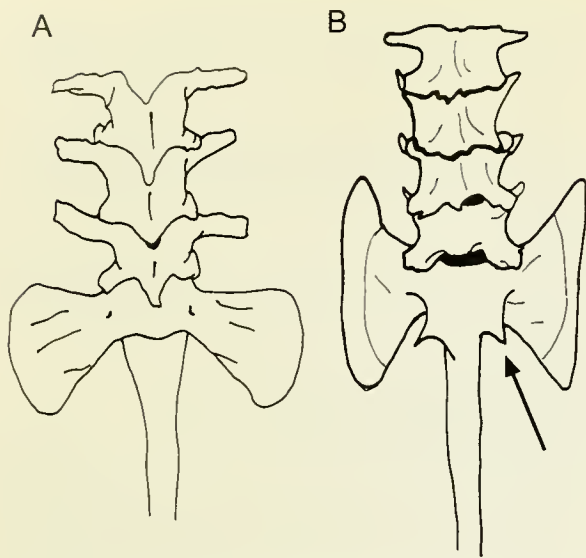
0: absent
1: present

Fig. 4. Dorsal view of the posterior presacral vertebrae, sacrum, and urostyle illustrating Character 44: "webbing" of sacrum/urostyle. (A) State 0.—*Discoglossus sardus* (KU 129239); (B) State 1.—*Spea multiplicata* (KU 86664). "Webbing" is denoted by arrow.

Postcranial Characters

Axial skeleton

39. Posterior extent of spinal processes.

    0: spinal processes reach the level of postzygapophyses

    1: spinal processes extend posteriorly beyond margin of postzygapophyses

40. Comparative length of transverse processes.—In many taxa, the transverse processes of Vertebra II are longer than those of the other presacral vertebrae.

    0: transverse process of Vertebra II longest

    1: transverse process of Vertebra II not longest

41. Uncinate processes on transverse process of Vertebra III.

    0: uncinate process of transverse process of Vertebra III absent

    1: uncinate process of transverse process of Vertebra III present

42. Lateral extent of transverse processes.

    0: transverse processes of Vertebrae V–VIII not extending beyond lateral margin of postzygapophyses

    1: transverse processes of Vertebrae V–VIII extending beyond lateral margin of postzygapophyses

43. Condition of sacral diapophyses.

    0: length of sacral diapophyses less than or equal to width

    1: length of sacral diapophyses longer than width, anterior and posterior ends rounded

    2: length of sacral diapophyses longer than width, anterior and posterior ends pointed

44. "Webbing" of sacrum/urostyle.—These are small bony plates that extend between the posteromedial margins of the sacral diapophyses and the urostyle (Wiens, 1989; Fig. 4). Although these have been considered to be postsacral transverse processes by some authors (e.g., Duellman and Trueb, 1986), Wiens (1989:48) suggested that they were homologous with the posterior webbing found on the presacral vertebrae.

    0: "webbing" of sacrum/urostyle absent

    1: "webbing" of sacrum/urostyle present

45. Fusion of ribs to transverse processes.—In the taxa examined, distinguishable ribs are present in larvae and adults of *Discoglossus sardus* and *Bombina orientalis*. Ribs are distinguishable in the larvae of *Xenopus laevis*, but are indistinguishably fused to the transverse processes of adults. Ribs are not distinguishable in all other taxa examined (including *Rhinophrynus dorsalis*).

    0: ribs distinguishable in larvae and adults

    1: ribs distinguishable in larvae only

    2: ribs not distinguishable in larvae or adults

46. Relative length of urostyle.—To determine the relationship of urostyle to presacral vertebrae lengths, these elements were measured on several individuals of each species and compared as an average ratio of snout-vent length. In all taxa considered, the combined length of the presacral vertebrae is about 35% SVL, and the urostyle length is as long as ($\cong$ 35% SVL) or much shorter than ($\cong$ 23% SVL) the combined length of the presacrals.

    0: urostyle as long or longer than combined length of presacral vertebrae

    1: urostyle shorter than combined length of presacral vertebrae

Anterior appendicular skeleton

47. Relative length of scapula.—To determine the relationship of scapula to coracoid lengths, these elements were measured on several individuals of each species and compared as an average ratio of snout-vent length. The relative length of the coracoid is similar among taxa (approximately 13% SVL). The relative length of the scapula is about the same in every taxon ($\cong$ 16% SVL); however, in *Discoglossus sardus, Pelodytes punctatus,* and *Xenopus laevis,* the scapula is relatively shorter ($\cong$ 7% SVL).

    0: scapula shorter than coracoid

    1: scapula slightly longer than coracoid

48. Bony sternum.—In the taxa considered, the sternum consists of a cartilaginous plate with or without a bony stylus (Fig. 5A, B).

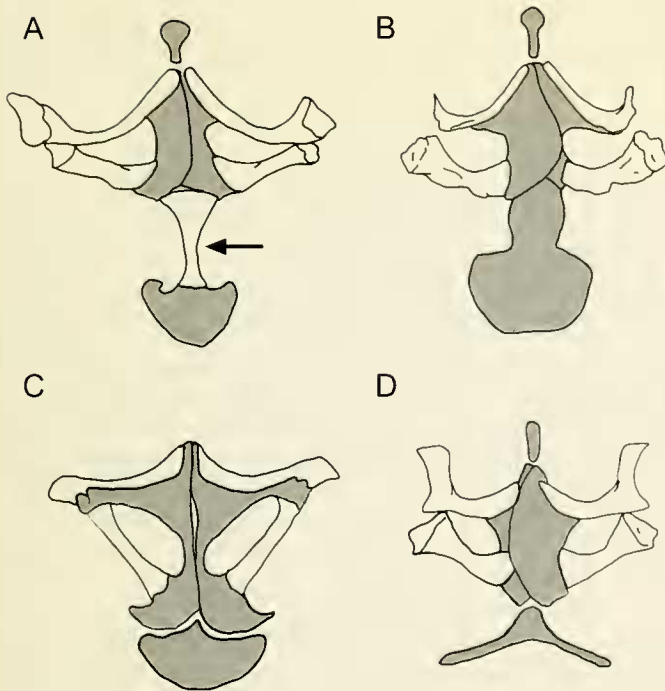   0: bony stylus absent

    1: bony stylus present

Fig. 5. Ventral view of the pectoral girdle with the scapula and suprascapula deflected, illustrating Character 48: bony sternum and Character 49: condition of sternal plate. (A) Character 48, State 1.—bony stylus present (indicated by arrow), and Character 49, State 1.—sternum forming elongate rod; *Pelobates cultripes* (MNCN 20241); (B) Character 48, State 0.—bony stylus absent, and Character 49, State 1.—sternum forming elongate rod; *Spea multiplicata* (KU 86662); (C) Character 49, State 2.—sternum forming semicircle with concave anterior margin; *Xenopus laevis* (KU 217969; redrawn from Trueb and Hanken, 1992); (D) Character 49, State 3.—sternum forming thin, sickle shape; *Discoglossus sardus* (KU 129239). Gray denotes cartilage, white denotes bone.

49. Condition of sternal plate.—In the taxa considered, the sternum consists of an elongate rod (with or without a rounded posterior portion), forms a semicircle with two concavities on the anterior margin, or forms a thin, sickle shape (Fig. 5).

    0: sternum absent
    1: sternum forming elongate rod (with or without rounded posterior plate)
    2: sternum forming semicircle with concave anterior margin
    3: sternum forming thin, sickle shape

50. Prezonal element.—When present, the prezonal element (= omosternum) is cartilaginous or ossified.

    0: absent
    1: cartilaginous
    2: ossified

51. Condition of pectoral girdle.—On most taxa, the pectoral girdle is arciferal, with the epicoracoid cartilages overlapping one another and the sternum attached (but not fused) to the pectoral arch. In *Limnodynastes*

flecheri and *Leptodactylus fuscus,* the epicoracoid cartilages are fused to one another, and the sternum is fused to the pectoral arch, in a typical firmisternal condition. In the pipoid taxa, the girdle is pseudofirmisternal—viz., the epicoracoid cartilages are not fused to one another, but there is less movement in the girdle relative to the arciferal condition.

    0: pectoral girdle arciferal
    1: pectoral girdle firmisternal
    2: pectoral girdle pseudofirmisternal

52. Calcification of sternum.—Disorganized calcium (identified by the presence of Alizarin Red staining) is deposited in the cartilaginous portion of the sternum in several taxa. This is distinct from Character 49, State 1: bony stylus.

    0: calcification of cartilaginous sternum absent
    1: calcification of cartilaginous sternum present

53. Curvature of long axis of coracoid.

    0: coracoid straight
    1: coracoid curved

54. Relative lengths of clavicle/coracoid.

    0: clavicle approximately equal in length to the coracoid
    1: clavicle much longer than coracoid

55. Condition of head of humerus.

    0: humeral epiphysis cartilaginous
    1: humeral epiphysis calcified

56. Torsion of first digit.—In most taxa examined, the first digit (= Digit II) of the forelimb is curved slightly toward the axis of the hand.

    0: torsion of Digit II absent
    1: torsion of Digit II present

Posterior appendicular skeleton

57. Dorsal crest on body of ischium.

    0: ischial crest absent
    1: ischial crest present

58. Epipubic cartilage.—When present, the epipubic cartilage is thin and rodlike, or forms an expanded plate.

    0: epipubic cartilage absent
    1: epipubic cartilage thin, rodlike
    2: epipubic cartilage forming an expanded plate

59. Condition of inner metatarsal tubercle.

    0: inner metatarsal tubercle not spadelike
    1: inner metatarsal tubercle spadelike, cuneiform
    2: inner metatarsal tubercle spadelike, elongate

Hyoid apparatus

60. Parahyoid bone.

    0: parahyoid absent
    1: parahyoid single, median
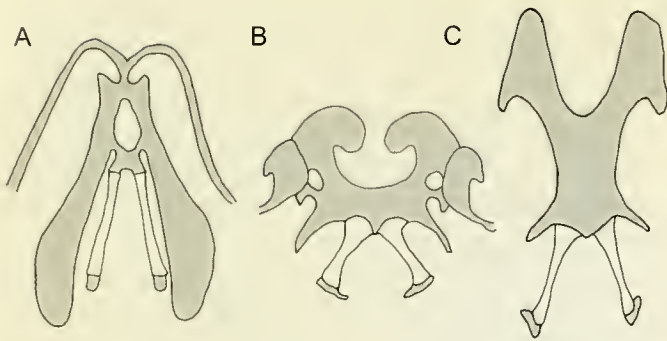   2: parahyoid paired, V-shaped

Fig. 6.   Ventral view of the hyoid apparatus illustrating Character 61: condition of the hyal. (A) State 0.—*Xenopus laevis* (KU 195935; redrawn from Cannatella, 1985); (B) State 1.—*Spea multiplicata* (KU 86662); (C) State 2.—*Leptobrachium haseltii* (KU 194712; redrawn from Cannatella, 1985). Gray indicates cartilage; white denotes bone.

61. Condition of hyal of hyoid (Fig. 6).

    0: hyal continuous, unbroken
    1: hyal divided, otic portion absent
    2: hyal divided, otic portion present

62. Alary process of hyoid.

    0: alary process of hyoid absent
    1: alary process of hyoid not fused to hyal
    2: alary process of hyoid fused to hyal, forming foramen for hypoglossal nerve

63. Condition of cricoid ring.
    0: cricoid ring complete
    1: cricoid ring divided dorsally

Myological and Soft-tissue Characters

These characters, states, and codings were taken directly from Cannatella (1985). Character states for *Leptodactylus fuscus* were coded from Limeses (1964) and Lynch (1969).

64. Adductor longus muscle.

    0: adductor longus absent
    1: adductor longus present

65. Condition of depressor mandibulae.

    0: origin of depressor mandibulae in part from fascia/bone of otic region
    1: origin of depressor mandibulae only from fascia over suprascapula

66. Accessory head of gracilis minor.

    0: accessory head of gracilis minor absent
    1: accessory head of gracilis minor present

67. Condition of piriformis muscle.

    0: piriformis present, thick
    1: piriformis reduced in thickness
    2: piriformis absent

68. Degree of exposure of sartorius and its tendon.

    0: sartorius and tendon superficial
    1: sartorius and tendon partially concealed by gracilis major

69. Ischiocutaneous muscle.

    0: ischiocutaneous absent
    1: ischiocutaneous present

70. Cloacal glands.

    0: cloacal glands absent
    1: cloacal glands present

71. Pectoral glands.

    0: pectoral glands absent
    1: pectoral glands present

72. Vocal sacs in adult males.

    0: vocal sacs absent
    1: vocal sacs present

Life-history Character

73. Condition of spiracle of tadpole.—In the taxa considered, the spiracle is either single or paired. When single, the spiracle is located at the ventral midline of the abdomen (= austral) or on the left side of the body (= sinistral).

    0: austral spiracle
    1: sinistral spiracle
    2: two spiracles

RESULTS

Analysis of the data matrix (Appendix) resulted in the discovery of six most parsimonious trees (Fig. 7), each 251 steps long, with a consistency index (CI) of 0.474 and a retention index (RI) of 0.653. Results (Fig. 7) indicate that the pelobatoids are the sister group of the pipoids and that Neobatrachia is the sister of [Pelobatoidea + Pipoidea]. Within the pelobatoids, Pelodytidae (represented by *Pelodytes*) is the sister group of Pelobatidae, and the Megophryidae is the sister taxon to [Pelobatidae + Pelodytidae]. The analysis also suggests that each of the three genera within the family Pelobatidae (*Pelobates*, *Scaphiopus*, and *Spea*) is monophyletic. The major differences among the six trees (Fig. 8) concern the relationships of the genera within Pelobatidae and the relationships of the species within *Pelobates*. The relationships within *Scaphiopus* could not be resolved with these data.

Retention indices (Bremer, 1988, 1994) and bootstrap values (over 50) for each node are presented in Figure 7. Note that the monophyly of the pelobatoids, neobatrachians, and pipoids was not tested, and therefore, no index is reported for these nodes. Each of the three genera within the Pelobatidae are fairly well supported. How-

ever, several clades have low levels of support, indicating that more data are likely to influence the relationships depicted in Figure 7, especially those with retention index values of 1.

DISCUSSION

RELATIONSHIPS WITH OTHER ANURANS

The analysis presented herein suggests that the Pelobatoidea (sensu Ford and Cannatella, 1993) is the sister taxon of the Pipoidea, and that the Mesobatrachia as defined by these authors (Pipoidea + Pelobatoidea) is a valid group. This is contrary to the hypotheses of Inger (1967) and Duellman and Trueb (1986) (Fig. 1), but supports the hypotheses of Cannatella (1985) and Laurent (1979). Support for the clade [Pelobatoidea + Pipoidea] is somewhat low (bootstrap value = 56; decay index = 2) and consists of two characters: dentigerous process of vomer anterior to planum antorbitale (Character 29, State 0), and the presence of a dorsal crest on body of the ischium (Character 57, State 1; also in *Leptodactylus fuscus*).

SUPPORT FOR PELOBATOIDEA

Although there have been numerous suggestions as to Pelobatoidea relationships, few studies have questioned the monophyly of the group (Lynch, 1973; Roček, 1980; Hillis, 1991). Although the monophyly of the group was not tested in this analysis, two characters seem to support Pelobatoidea as a natural group: sinistral spiracle in tadpoles (Character 73, State 1; also in *Limnodynastes fletcheri*) and pathway for occipital vessels roofed in bone (Character 5, State 1; not in *Pelodytes punctatus*).

INTERFAMILIAL RELATIONSHIPS

This analysis suggests that within the pelobatoids, Pelobatidae is the sister taxon of Pelodytidae (represented by *Pelodytes punctatus*); this supports the hypothesis of Cannatella (1985) (Fig. 1). Several authors (e.g., Kluge and Farris, 1969; Savage, 1973) also suggested a sister relationship of the pelobatids and pelodytids and recognized the pelodytids as part of the Pelobatidae. My findings are contrary to the hypotheses of Henrici (1994), Lynch (1973), and Duellman and Trueb (1986) who supported the megophryids as sister of the pelobatids by recognizing Megophryinae, a subfamily within Pelobatidae, and Pelodytidae as a separate family.

Several characters support the clade [Pelobatidae + Pelodytidae]: origin of the depressor mandibulae from the fascia over the suprascapula (Character 65, State 1); alary process of the hyoid fused and forming a foramen for hypoglossal nerve (Character 62, State 2); hyal of hyoid divided, otic portion present (Character 61, State 2; also in *Rhinophrynus dorsalis*); transverse processes of Presacral II longer than other transverse processes (Character 40, State 0; also in *Discoglossus sardus*); and presence of an accessory head of the gracilis minor muscle (Character 66, State 1; also in *Rhinophrynus dorsalis*).

Cannatella (1985) suggested that the family Pelobatidae, including the subfamilies Pelobatinae and Megophryinae, is paraphyletic. Therefore, he suggested elevating the subfamily Megophryinae to the family Megophryidae, a suggestion followed by many subsequent authors (e.g., Ford and Cannatella, 1993; Lathrop, 1997). However, neither Cannatella's (1985) nor Ford and Cannatella's (1993) analyses unequivocally supported the paraphyly of Pelobatidae. Results of the present analysis show that the Pelobatidae and Megophryidae are not sister taxa and support the recognition of the family Megophryidae.

RELATIONSHIPS WITHIN THE PELOBATIDAE

Among genera.—The strict consensus of the six most parsimonious trees indicates that the relationships within the Pelobatidae are unresolved (Fig. 7); however, four of these six trees (as indicated by the 50% majority rule tree; Fig. 8) indicate that *Pelobates* and *Scaphiopus* are sister-taxa, and that *Spea* is the sister of the combined clade [*Pelobates* + *Scaphiopus*]. This is contrary to all hypotheses presented thus far (e.g., Cannatella, 1985; Henrici, 1994), and in fact, most authors recognize *Spea* as a subgenus of *Scaphiopus* (e.g., Zweifel, 1956; Sage et al., 1982; Duellman and Trueb, 1986). The clade [*Pelobates* + *Scaphiopus*] is supported by several characters, all but one of which have some level of homoplasy: the presence of ornamentation on the frontoparietals, nasals, maxillae, premaxillae, and squamosals (Character 1, State 1); frontoparietals in contact with nasals (Character 4, State 1; also in *Discoglossus sardus* and pipoid taxa); presence of a supraorbital flange of the frontoparietal (Character 2, State 1; also in *Megophrys montana* and *Rhinophrynus dorsalis*); presence of a well-developed maxillary process of the nasal (State 1; also in *Leptobrachium haseltii*, *Discoglossus sardus*, and *Bombina orientalis*); presence of a pterygoid process of the maxilla (Character 24, State 1; also in *Megophrys montana*, *Rhinophrynus dorsalis*, *Leptodactylus fuscus*, and *Discoglossus sardus*); presence of a ventral flange of the anterior ramus of the pterygoid (Character 33, State 1; also in *Xenopus laevis*, *Leptodactylus fuscus*, and *Discoglossus sardus*); otic ramus of the squamosal forming otic plate (State 1; also in the megophryid taxa); long zygomatic ramus of the squamosal (Character 36, State 1; also in *Leptodactylus fuscus* and *Discoglossus sardus*); spinal processes extending posteriorly beyond the margin of postzygapophyses (Character 39, State 1; also in *Leptobrachium haseltii*, pipoid taxa, and *Discoglossus sardus*); and inner metatarsal tubercle present, spadelike, cuneiform (Character 59, State 1; also in *Rhinophrynus dorsalis*).
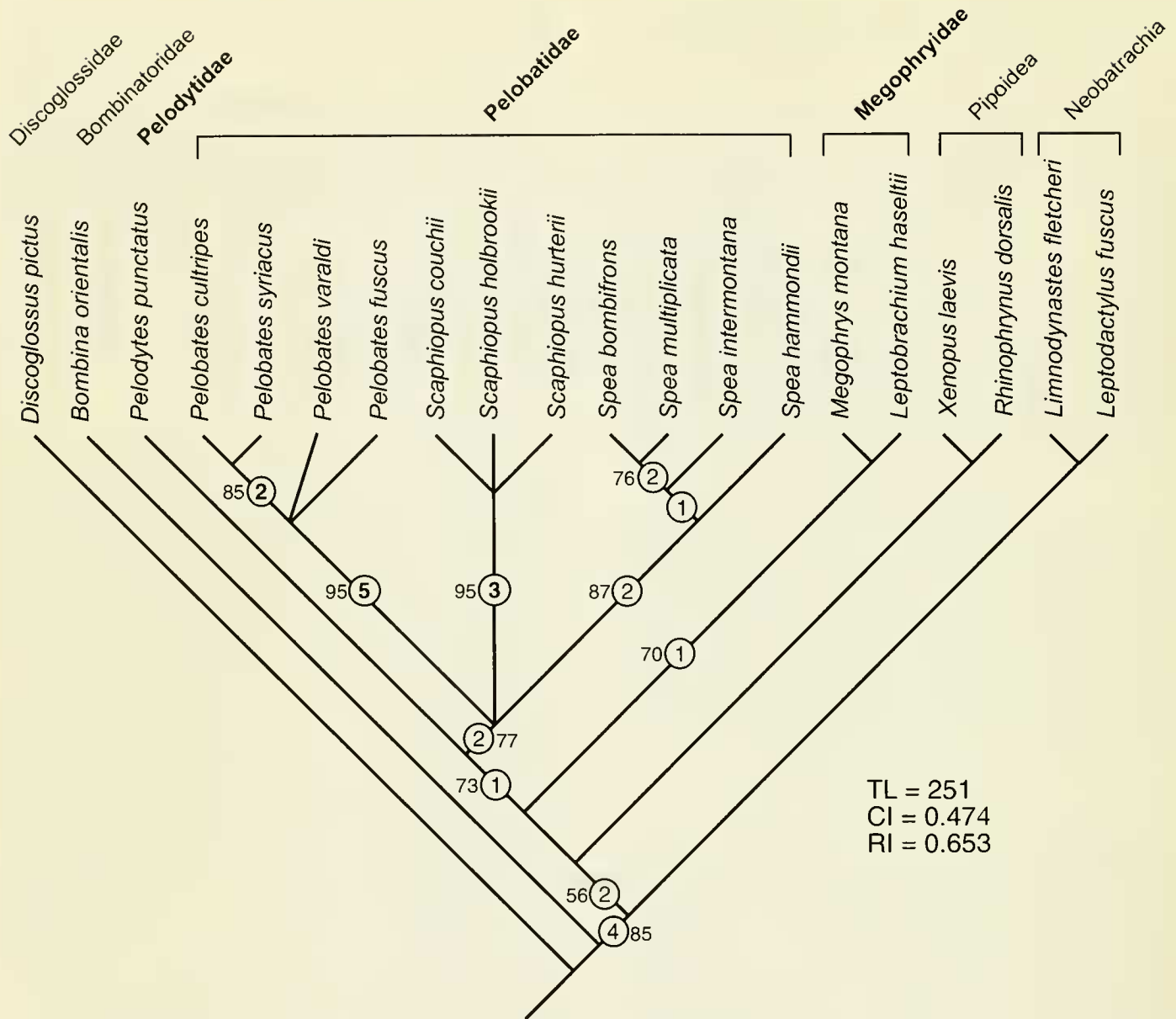
Fig. 7. Strict consensus of the six most parsimonious trees resulting from a heuristic analysis of the data matrix of 73 morphological characters. Numbers in circles refer to Bremer decay indices; numbers not circled refer to bootstrap values (> 50). TL = total length; CI = consistency index; RI = retention index. Pelobatoid families are in boldface.

The topology of the remaining two equally most parsimonious trees suggests the relationship [*Spea + Scaphiopus*]. This hypothesis is supported by several characters: palatine process of the maxilla not distinct from vomer (Character 25, State 0); absence of calcification of the sternum (Character 52, State 0; also in pipoids and *Discoglossus sardus*); sartorius muscle partially concealed by the gracilis major muscle (Character 68, State 1); long axis of the coracoid curved (Character 53, State 1); absence of a bony stylus of the sternum (Character 48, State 0; Fig. 5B; also in *Pelodytes punctatus*, megophryids, and *Leptodactylus fuscus*); sacral diapophyses longer than wide and rounded (Character 43, State 1; also in *Bombina orientalis*); absence of a quadratojugal (Character 38, State 0); and postchoanal process of the vomer elongate (Character 28, State 2).

Based on comparisons of the characters supporting these hypotheses, the low support index for the node [*Pelobates + Scaphiopus*], and the geographic distribution of the taxa concerned (*Spea* and *Scaphiopus* in North
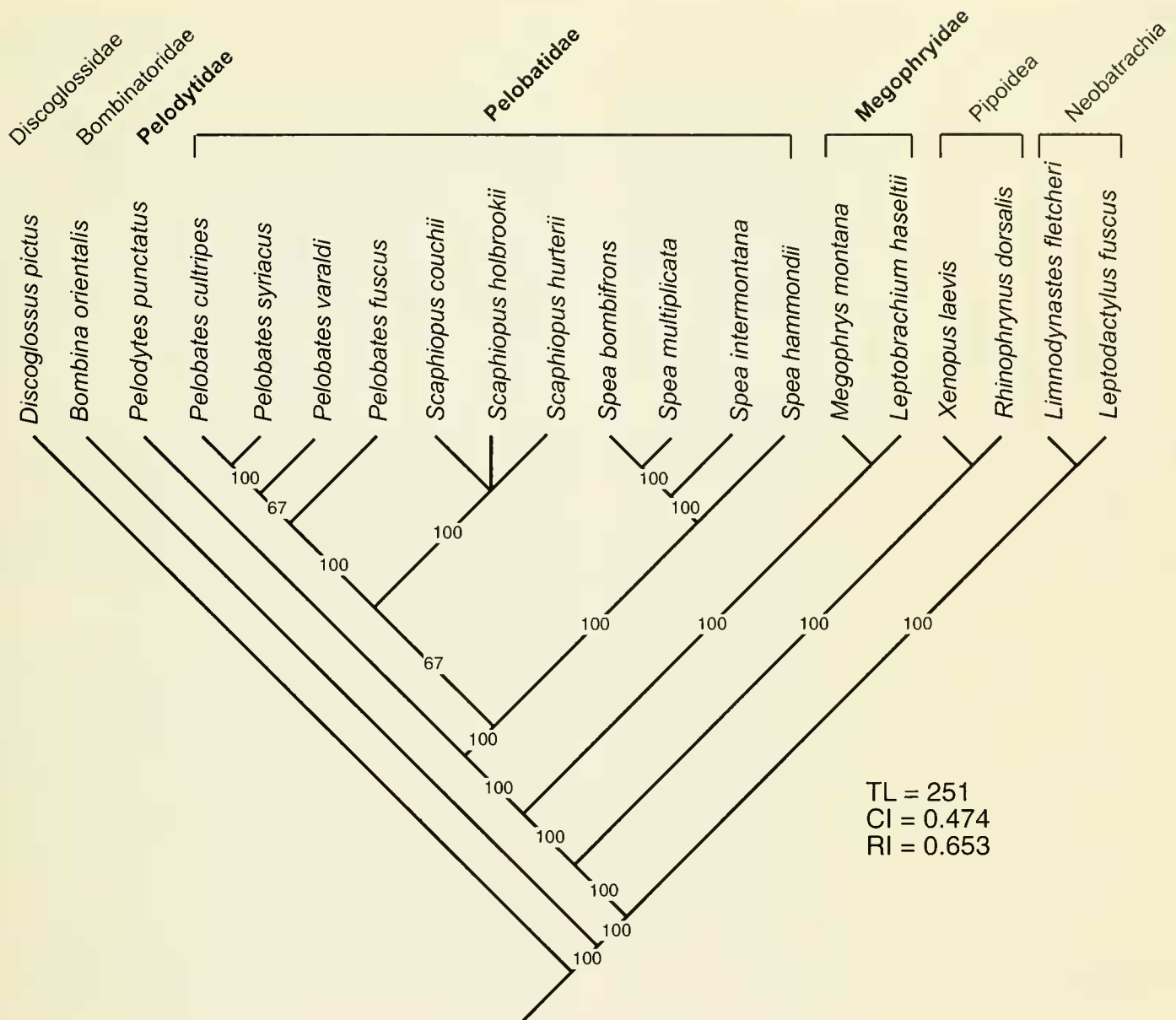
Fig. 8.   Majority rule consensus of the six most parsimonious trees. TL = total length; CI = consistency index; RI = retention index. Pelobatoid families are in boldface.

America, *Pelobates* in Europe and northern Africa), it is difficult to lend much confidence to the purported sister relationship of *Pelobates* and *Scaphiopus*. Instead, I speculate that the hypothesized relationship [*Pelobates* + *Scaphiopus*] is a result of homoplasy. Both *Scaphiopus* and *Pelobates* are highly ossified with broad, ornamented skulls. *Spea* lacks much of this ossification, and some species have reduced ossification (e.g., *Spea intermontana*). Therefore, it seems likely that many of the characters supporting the grouping [*Pelobates* + *Scaphiopus*] actually support the monophyly of Pelobatidae and have reversed in *Spea*. This argument

is supported by Wiens' (1989) contention that many of the synapomorphies uniting *Spea* are the result of paedomorphosis. More characters, particularly those that do not relate to degree of cranial ossification (e.g., larval skeleton, molecular) are needed to resolve this issue.

Within *Pelobates*.—The monophyly of *Pelobates* is well supported (Fig. 7) by several synapomorphies, three of which are unequivocal: presence of a foramen in the lamina perpendicularis of the frontoparietal (Character 7, State 1); absence of a piriformis muscle (Character 67, State 2); and presence of an auxiliary dorsal process of the pterygoid

(Character 34, State 1). Several other characters, all with some level of homoplasy, support *Pelobates* as a natural group: the presence of uncinate processes on Vertebra III (Character 41, State 1; also in *Discoglossus sardus* and the neobtrachian taxa); urostyle shorter than combined length of presacral vertebrae (Character 46, State 1; also in *Pelodytes punctatus*, *Leptobrachium haseltii*, *Rhinophrynus dorsalis*, and *Limnodynastes fletcheri*); absence of a posteromedial process of the parasphenoid (Chracter 27, State 0; also absent in *Spea bombifrons*, *S. multiplicata*, and *Bombina orientalis*); and frontoparietal fused, no suture, three centers of ossification (Character 3, State 5). Also, eight other characters (equivocal at node Pelobatidae and/or Pelobatidae + *Pelodytes*), with various amounts of homoplasy, may be synapomorphies for *Pelobates*: (1) Character 23, State 0; (2) Character 28, State 1; (3) Character 38, State 1; (4) Character 43, State 2; (5) Character 48, State 1; (6) Character 53, State 0; (7) Character 52, State 1; and (8) Character 25, State 1.

Within *Pelobates*, the relationships among the species are fully resolved. The hypothesis presented herein suggests that *P. cultripes* and *P. syriacus* are sister taxa, which is supported by a wide alary process of the premaxilla (Character 12, State 1; also in *Spea*, the megophryids, pipoids, and neobatrachians) and the presence of 16 premaxillary teeth (Character 15, State 5). Results also suggest that *P. varaldii* is the sister to the combined clade [*P. cultripes* + *P. syriacus*], based on the contact of the squamosal and frontoparietal (Character 37, State 1) and the presence of a postorbital process of the maxilla (Character 20, State 1; also in *Scaphiopus*, *Megophrys montana*, and *Discoglossus sardus*).

The results of this analysis differ from both Cannatella's (1985) hypothesis and the reanalysis of his data set by Lathrop (1997). Cannatella (1985) suggested the sister relationships of *Pelobates fuscus* and *P. syriacus*; his analysis did not resolve their relationships with the other two species. Lathrop (1997) showed the grouping [*P. fuscus* + *P. syriacus*], with *P. cultripes* as the sister to this combined clade and *P. varaldii* as the sister to [(*P. fuscus* + *P. syriacus*) + *P. cultripes*].

Within *Scaphiopus*.—The monophyly of *Scaphiopus* is well supported, based on at least three synapomorphies, including the following: absence of an adductor longus muscle (Character 64, State 0; also absent in the pipoids and *Bombina orientalis*); presence of an ischiocutaneous muscle (Character 69, State 1; also present in *Rhinophrynus dorsalis*); and the presence of a lingual process of the premaxilla (Character 13, State 1; also in *Spea multiplicata*, *Xenopus laevis*, and the neobatrachians).

Within *Scaphiopus*, the relationships are unresolved. Other authors (e.g., Cannatella, 1985; Lathrop, 1997) have

suggested that *Scaphiopus holbrookii* is the sister taxon to *S. hurterii*, and that *Scaphiopus couchii* is the sister to the combined clade [*S. holbrookii* + *S. hurterii*]. This reflects the fact that *S. holbrookii* and *S. hurterii* have been recognized as the same species by some authors (e.g., Sage et al., 1982; Frost, 1985). Difficulty in resolving the relationships of these species comes from *Scaphiopus holbrookii* sharing three separate characters with both *S. couchii* and *S. hurterii*. Characters supporting [*S. holbrookii* + *S. couchii*] include: anterior margin of prootic foramen partially formed by bone (Character 31, State 1; also in *Pelobates fuscus* and *Limnodynastes fletcheri*); the maxilla not extending for most of the length of the orbit (Character 18, State 0; also in *Spea* and *Xenopus laevis*); and the pars palatina of the premaxilla broadening laterally (Character 14, State 1; also in *Leptobrachium haseltii*, *Rhinophrynus dorsalis*, *Leptodactylus fuscus*, and *Bombina orientalis*). Characters supporting the grouping [*S. holbrookii* + *S. hurterii*] are: and the presence of pectoral glands (Character 71, State 1); the presence of 50 maxillary teeth (Character 19, State 8; also in *Spea hammondii* and *Leptodactylus fuscus*); and the presence of a raised ridge on the parasphenoid (Character 26, State 1; also in *Pelobates varaldi* and *Megophrys montana*).

Within *Spea*.—The monophyly of *Spea* is supported by several characters, including: the presence of cloacal glands (Character 70, State 1); a spadelike, elongate inner metatarsal tubercle (Character 63, State 2); the presence of a maxillary foramen (Character 23, State 1; also in *Scaphiopus hurterii*); a pointed anterior process of the nasal (Character 10, State 1); the anterior margin of the prootic foramen formed completely by bone (Character 31, State 2; also in the pipoid taxa and *Leptodactylus fuscus*); the maxilla not extending posteriorly beyond half the length of the orbit (Character 18, State 0; also in *Scaphiopus couchii*, *S. holbrookii*, and *Xenopus laevis*), and the septum nasi forming an anterior bony plate (Character 17, State 2; also in *Pelobates fuscus*, *Xenopus laevis*, and *Leptodactylus fuscus*; plate absent in *Spea multiplicata*).

Within the genus *Spea*, the relationships among taxa are fully resolved. *Spea bombifrons* and *S. multiplicata* are sister taxa. This is supported by the absence of a posteromedial process of the parasphenoid (Character 27, State 0; also in *Pelobates* and *Bombina orientalis*), a short zygomatic ramus of the squamosal (Character 35, State 1; also in *Megophrys montana* and *Limnodynastes fletcheri*), and the presence of 12 premaxillary teeth (Character 15, State 2; also in *Leptobrachium haseltii*). *Spea intermontana* is the sister taxon to the clade [*S. bombifrons* + *S. multiplicata*] based on the absence of medial contact of the nasals (Character 8, State 0; also in *Pelodytes punctatus*, *Leptobrachium haseltii*, *Bombina orientalis*, and *Discoglossus sardus*).

Neither Cannatella's analysis (1985) nor the reanalysis of his data matrix (Lathrop, 1997) provided resolution of

the relationships within the genus *Spea*. However, Wiens and Titus (1991) conducted a phylogenetic analysis of this genus using allozyme and morphological data. Their results differ from those presented herein in that they found *Spea intermontana* to be paraphyletic, with populations in Colorado as the sister to *S. bombifrons*, and populations in Oregon as the sister to this combined clade. They showed that *S. hammondii* is the sister to [(*S. intermontana*-Colorado + *S. bombifrons*) + *S. intermontana*-Oregon] and that *Spea multiplicata* is the basal taxon in the group. Differences between Wiens and Titus' (1991) hypothesis and the one presented herein may be because of homoplasy in the morphological and/or allozymic characters used in the analyses.

CONCLUSIONS

Although many of the pelobatoid relationships presented herein are resolved, several of the proposed nodes lack strong support (Fig. 7), and some groupings (e.g., *Scaphiopus* + *Pelobates*; relationships within *Spea*) conflict with all other proposed hypotheses. Therefore, although this analysis has provided a basic framework for understanding the relationships among extant pelobatoids, more

data are needed to generate a robust phylogenetic hypothesis. Because of the known homoplastic nature of characters dealing with the amount of cranial ossification in these taxa (e.g., *Scaphiopus* and *Pelobates*), particular focus should be given to the study of larval skeletons and ontogenetic trajectories, both to search for characters that are not correlated with degree of ossification and as a way of understanding the homology of adult characters. Also, for taxonomic completeness and in the search for new synapomorphies, the characters presented herein should be coded from the numerous pelobatoid fossils (a task partially completed by Henrici [1994]).

The purpose of this paper was not to resolve fully the relationships of the pelobatoids, but rather to lay down a foundation for which future studies may be conducted. By summarizing and redefining morphological characters that historically have been used in the study of extant pelobatoid systematics and coding new and informative morphological characters, I hope to have created a framework in which information from fossil pelobatoids, larval skeletons and development, and molecular data can be added and compared both practically and beneficially.

LITERATURE CITED

Brattstrom, B. H. 1957. The phylogeny of the Salientia based on skeletal morphology. Systematic Zoology 6:70–74.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10:295–304.

Cannatella, D. C., 1985. *A Phylogeny of Primitive Frogs (Archaeobatrachians)*. Doctoral dissertation. Lawrence: The University of Kansas. 404 pp.

Dubois, A. 1983. Classification et nomenclature supragénérique des amphibiens anoures. Bulletin Mensuel de la Société Linnénne de Lyon 52:270–276.

Duellman, W. E. 1975. On the classification of frogs. Occasional Papers of the Museum of Natural History of The University of Kansas 42:1–15.

Duellman, W. E. 1988. Evolutionary relationships of the Amphibia. Pp. 13–34 in Fritzch, B. (ed.) *The Evolution of the Amphibian Auditory System.* New York: John Wiley and Sons. 705 pp.

Duellman, W. E. and L. Trueb. 1986. *Biology of the Amphibians.* New York: McGraw-Hill Book Co., 670 pp.

Evans, S. E., and A. R. Milner. 1993. Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. Journal of Vertebrate Paleontology 13:24–30.

Ford, L. S., and D. C. Cannatella. 1993. The major clades of frogs. Herpetological Monographs 7:94–117.

Frost, D. R., (ed.). 1985. *Amphibian Species of the World.* Lawrence, Kansas: Allen Press and the Association of Systematics Collections, iv + 732 pp.

Griffiths, I. 1963. The phylogeny of the Salientia. Biology Review 38:241–292.

Hay, J. M., I. Ruvinsky, S. B. Hedges, and L. R. Maxon. 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. Molecular Biology and Evolution 12:928–937.

Hillis, D. M. 1991. The phylogeny of amphibians: current knowledge and the role of cytogenetics. Pp. 7–31 in D. M. Green and S. K. Sessions (eds.) *Amphibian Cytogenetics and Evolution.* San Diego: Academic Press, 456 pp.

Henrici, A. C. 1994. *Tephrodytes brassicarvalis*, new genus and species (Anura: Pelodytidae), from the Arikareean Cabbage Patch beds of

Montana, USA, and pelodytid–pelobatid relationships. Annals of the Carnegie Museum 63:155–183.

Inger, R. F. 1967. The development of a phylogeny of frogs. Evolution 21:369–384.

Kluge, A. G. 1966. A new pelobatine frog from the lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. Contributions in Science, Los Angeles County Museum 113:1–26.

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18:1–32.

Lathrop, A. 1997. Taxonomic review of the megophryid frogs (Anura: Pelobatoidea). Asiatic Herpetological Research 7:68–75.

Laurent, R. F. 1979. Esquisse d'une phylogenese des anoures. Bulletin Society Zoology, France 104:397–422.

Limeses, C. E. 1964. La musculatura del muslo en los Ceratofrínidos y formas afines, con un análisis crítico sobre la significacíon de los caracteres miológicos en la sistemática de los Anuros superiores. Universidad de Buenos Aires Facultad de Ciencias Exactas y Naturales Contribuciones Cientificas, Serie Zoologia 1(4):193–245.

Lynch, J. D. 1969. *Evolutionary Relationships and Osteology of the Frog Family Leptodactylidae.* Doctoral dissertation. Lawrence: The University of Kansas, 404 pp.

Lynch, J. D. 1973. The transition from archaic to advanced frogs. Pp. 133–182 in J. L. Vial (ed.), *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems.* Columbia: University of Missouri Press, vii + 470 pp.

Maglia, A. M. (In press.) The Adult Skeleton of *Spea multiplicata* and a Comparison of the Osteology of the Pelobatid Frogs (Anura: Pelobatidae). Alytes.

Mendelson, J. R., III, H. R. da Silva, and A. M. Maglia. (In press.) Phylogenetic relationships among marsupial frog genera (Anura: Hylidae: Hemiphractinae) based on evidence from morphology and natural history. Zoological Journal of the Linnean Society.

Noble, G. K. 1931. *The Biology of the Amphibia.* New York: McGraw-Hill Co., 577 pp.

Orton, G. L. 1953. The systematics of vertebrate larvae. Systematic Zoology 2:63–75.

Reig, O. A. 1958. Proposiciones para una nueva macrositemática de los

anuros. Physis 21:109–118.

Roček, Z. 1980. Cranial anatomy of frogs in the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. Acta Universitatis Carolinae Biologica 3:1–164.

Sage, R. D., E. M. Prager, and D. B. Wake. 1982. A Cretaceous divergence time between pelobatid frogs (*Pelobates* and *Scaphiopus*): Immunological studies of albumin serum. Journal of Zoology, London 198:481–494.

Savage, J. M. 1973. The geographic distribution of frogs: Patterns and predictions. Pp. 351–445 *in* J. L. Vial (ed.), *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems.* Columbia: University of Missouri Press, vii + 470 pp.

Sokal, O. M. 1977. A subordinal classification of frogs (Amphibia: Anura). Journal of Zoology, London 182:505–508.

Starrett, P. H. 1973. Evolutionary patterns in larval morphology. Pp. 251–271 *in* J. L. Vial (ed.), *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems.* Columbia: University of Missouri Press, vii + 470 pp.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Champaign: Illinois Natural History Survey.

Trueb, L., and J. Hanken. 1992. Skeletal development in *Xenopus laevis* (Anura: Pipidae). Journal of Morphology 214:1–41.

Wiens, J. J. 1989. Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae). Journal of Morphology 202:29–51

Wiens, J. J., and T. A. Titus 1991. A phylogenetic analysis of *Spea* (Anura: Pelobatidae). Herpetologica 47:21–28.

Zweifel, R. G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and Recent forms. American Museum Novitates 1762:1–45.

APPENDIX

DATA MATIX

	1	2	3
Species	1234567890	1234567890	1234567890

Species	Data matrix
Discoglossus sardus	0011000000 1000000014 1100110111 0111190110
Bombina orientalis	0000000001 0010000111 0111001001 1001140000
Pelodytes punctatus	0000000010 0000011012 0010010111 1030010
Megophrys montana	0110100110 0100031019 1100111102 0010
Leptobrachium haseltii	0020100010 1012101901 0001011000 010
Xenopus laevis	0041000100 0110112020 0000020100 07221
Rhinophrynus dorsalis	0141000100 0101211170 1101201100 0200
Limnodynastes fletcheri	0010000100 0110400170 1100201115 110
Leptodactylus fuscus	0020000100 0111012190 0101101182 11
Pelobates cultripes	1151101100 1005001711 1011000106 0?1
Pelobates fuscus	1151101110 1000102160 1101100105 131
Pelobates syriacus	1151101100 1000101151 1101110010 4031
Pelobates varaldii	1151101100 1000101151 1011101030 11
Scaphiopus couchii	1131100100 0101160108 1110100120 311
Scaphiopus holbrookii	1131100100 0101170109 1111011201 11
Scaphiopus hurterii	1131100100 1010080119 1111112070 11
Spea bombifrons	0010110010 1002020300 1110000202 2210
Spea hammondii	0010101010 1000602090 1100012032 101
Spea intermontana	0010110001 0100112000 1120001201 2
Spea multiplicata	0010100011 0120100501 1100002032 1